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Free cells of plants and animals can readily be seen from all sides. Though varying greatly in form they are regarded as primarily spherules or globules, easily flattening into discoids, or elongating to form ellipsoids and rods of varying length with rounded ends. But the shape which such cells assume when surrounded and compressed by similar cells, though frequently a subject for inference, has apparently never been determined by the observation of actual cells, and on this supposition the present study was undertaken. Even though the examination of many sorts of cells for this purpose is very difficult, and in the most favorable cases is tedious, it seems impossible that such work has not already been done. But if so, it remains unknown to the writer, after some inquiry and a search of the literature at hand.

Previous publications record and reiterate that the problem of cell-shape is solved in foam. In the earliest observations, Robert Hooke found that within the shaft of a feather the cells form "a kind of solid or hardened froth, or a congeries of very small bubbles," [1] and Grew described parenchyma as "much the same thing, as to its conformation, which the froth of beer or eggs is." Two centuries later, Errera remarks that cell-walls "must correspond with such a lamellar system as one gets in pouring soap-suds, beer, etc. from a narrow-necked bottle." Clearly these bubbles are not cubes; and although Grew ascribed cubical cells to the pith of "reed-grass," and at present epithelial cells of a certain type are commonly called "cuboidal," it appears that true cubical cells have never been shown to occur, even as rare exceptions.

Parenchymal cells which are "pentangular, sexangular, and septangular" were seen by Grew, and the prevailing hexagonal form of such cells in section is shown in some of his figures. Cut tangentially, the cells of cork were found by Hooke to be as regularly hexagonal as

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1 Schwann, in his *Mikroskopische Untersuchungen*, Heft 1, 1838, p. 94, confirmed the accuracy of Hooke's comparison of the cells in the pith of a feather with those of cork, but without citing the earlier work.

cells in honeycomb. If these cells should be six-sided tubes divided into little boxes by transverse diaphragms, as he described them, octahedral shapes would be produced; though if the diaphragms in adjacent cells stand at different levels, something more complicated is at once suggested.

In 1812, Dr. Dieterich Georg Kieser, professor of medicine at Jena and collaborator with Oken, obtained the Teylerian prize for an essay on the structure of plants. It seems that he had not then reached the conclusion published in his Phytotomie (1815) that "the higher plant consists of a mass of individual cells — cell-tissue — and the cells then assume, through mutual pressure, a form determined by mathematical laws and consequently inevitable, namely that of the *rhombic dodecahedron*." [2] He considered that this dodecahedron may have the proportions shown in Figure 1, *a*; or it may be either flattened or elongated (Figure 1, *b*). In Oken's Physiophilosophy it is declared dogmatically that the fundamental form of cells is the rhombic dodecahedron, with Kieser as authority; and its production is explained somewhat as follows. If spheres are stacked (after the manner of cannon balls) any one will rest in a depression between three which are below it; it will be surrounded by six in its equatorial region; and there will be three more in contact with it at the upper pole — twelve altogether. The model of such a cell may readily be made from balls of putty or plasticine, which by compression become rhombic dodecahedra, and it will be similar to Figure 1, *a*, but rotated so that trihedral angles are at the top and bottom respectively. Or, following the suggestion of Buffon, dry peas may be packed close in a jar and tightly secured by wire netting, after which they are made to swell until all the interstices are obliterated, by placing them in boiling water. The peas so treated are usually irregular little dodecahedra, though peas with eleven or thirteen contacts are not infrequent.[3]

An interesting feature of Kieser's work, often overlooked, is illustrated in Figure 1, *c* and *d*. He considered that truncate rhombic

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[2] Although Kieser cites no previous authorities, he may not have been the first to consider vegetable cells as dodecahedral. Allman is said to have made the suggestion, in regard to cells of dicotyledons, in a paper read before the Royal Society in 1811 and privately printed (Thompson, *Growth and Form*, p. 643). But it was through Kieser's exposition that the idea became generally and favorably known. Thus Schleiden (Müller's Archiv, 1838, p. 146) remarks that "the form of cells frequently passes into that of the rhombic dodecahedron, so beautifully determined a priori by Kieser."

[3] Buffon did not describe the shape of peas, "or better, some cylindrical seed," treated in this way further than to remark that the cylinders become hexagonal prisms. This was in connection with his study of the form of cells in honeycomb. The entire passage has been quoted by Thompson, p. 333–334.

dodecahedra occur more often than the typical form. The upper and basal surfaces of such cells are hexagonal instead of quadrilateral, and the two quadrilaterals which previously extended from the base to the top likewise become hexagons. Such a form, with four hexagonal and eight quadrilateral surfaces, Kieser regarded as typical for the parenchyma of bark and pith, being impressed with the way in which it provided hexagonal sections when cut in several planes. The flattened form (Figure 1, *d*) will be seen to be a most interesting approximation to the shape of cells actually found by methods not at Kieser's disposal. In an excellent diagrammatic figure he showed how the truncate dodecahedra would appear when combined to make a tissue, and this perhaps led DeCandolle to warn his readers that "cells are not as regular as the published figures might lead one to believe."

Thus the matter rested until Plateau, in 1873, brought together his masterly researches on the statics of liquids. By means of wire frames dipped in glycerinated or soapy solutions he produced "liquid polyhedra," studying the production and arrangement of the films which make their walls. In 1886 this work in physics was applied to the problem of cell forms both by Berthold in his *Studien über Protoplasmamechanik* and by Errera, *Ueber Zellenformen und Seifenblasen.* Neither writer discloses the shape of parenchymal cells — Errera refers to the endless diversity of cell forms — but the inclination and curvature of cell walls, as seen in sections, are carefully studied, and compared with inert liquid films and "artificial cell-tissues." It is concluded that the phenomena of surface tension are of controlling importance in the shaping of cells.

In accordance with the mathematics of his time, Kieser had declared that, of all bodies which may be combined to fill space without interstices, "the rhombic dodecahedron encloses the greatest space with the least extent of surface." But in 1887, Lord Kelvin, after experimenting with Plateau's cubic skeleton frame, demonstrated that for the division of space with minimal partitional area the rhombic dodecahedron is rivaled by a more stable tetrakaidecahedron, or figure having fourteen surfaces, certain of which are slightly curved. Neglecting the curvature of such films, which he calculated with precision, as being lost in greater curves and irregularities due to shrinkage in preserved tissue, the form of this tetrakaidecahedron deserves careful attention. It has six quadrilateral and eight hexagonal surfaces, which form "thirty-six edges of intersection between faces, and twenty-four corners, in each of which three faces intersect." If the quadrilateral surfaces are equal squares, and the hexagons are equal, equilateral and equiangular hexagons, the figure becomes what Lord

Kelvin, in his Robert Boyle and Baltimore Lectures, called an "orthic tetrakaidecahedron." Such a solid has been drawn in Figure 1, *e–i*. It has already been stated that there is reason to consider the top and bottom of the cell as hexagonal, the sides and angular points of one of these hexagons being perpendicularly above or below those of the other. If this is done, Figure 1, *e*, represents either the top or basal view of the solid, seen in projection and not in perspective. The central hexagon is surrounded by alternating squares and hexagons — three of each. A lateral view, with a side and not an angle of the top and basal hexagons toward the observer, is shown in Figure 1, *f*. To pass from the top to the bottom, two surfaces must be traversed,— a square with a hexagon below it, or a hexagon with a square below it. A lateral view, with an angle of the top and basal hexagons toward the observer, is seen in Figure 1, *g*. If, instead of a hexagon, one of the squares should be regarded as the top, then the solid, seen from above, would appear as in Figure 1, *h*.[4] The lateral view with an angle of the square toward the observer has precisely the same appearance; but if a side of the square is toward us, the lateral aspect is as in Figure 1, *i*, which is the same as Figure 1, *g*, turned about. These, then, are the appearances to be sought in actual cells if they possess the tetrakaidecahedral form. The way in which such solids combine to fill space is shown in Figure 3 (Plate 1).

A further and very instructive review of the literature has been provided by D'A. W. Thompson, but it leaves him unable to decide whether the cells of vegetable parenchyma are dodecahedra or tetrakaidecahedra. He finds that these cannot be distinguished in ordinary sections, but suggests that it might be done through maceration. "Very probably," he concludes, "it is after all the rhombic dodecahedral configuration which, even under perfectly symmetrical conditions, is generally assumed."

Maceration appears to be impracticable,[5] but there is no special difficulty in reconstructing, by Born's familiar wax-plate method,

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[4] In this view the solid is seen to be a cube strongly truncated by an octahedron. Any mineral which crystallizes in the isometric system is capable of exhibiting such a combination, and it is not uncommon in gold, galena, pyrite, salt, fluorite, cuprite and diamond. But the truncating of the cube by the octahedron, or vice versa, in crystals is often slight, and the faces are usually unequal, so that the production of an orthic tetrakaidecahedron would be very rare indeed. For this information the writer is much indebted to Professor B. L. Robinson and Professor Palache. Crystals of alum, however, may be nearly orthic as seen, for example, in Figure 548, Plate 70, of Adams' *Micrographia* (4th ed., London, 1771).

[5] M. H. Dutrochet (Recherches . . . sur la structure intime des animaux et

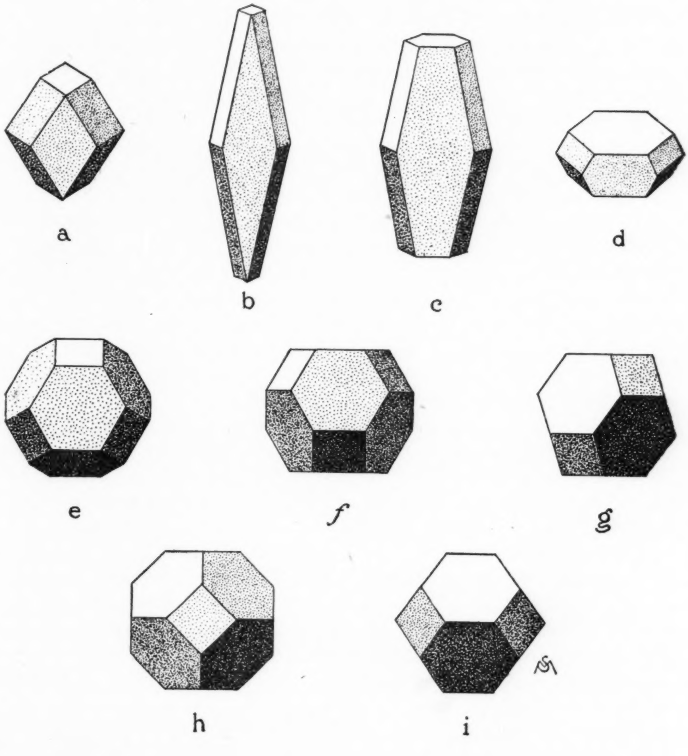


FIGURE 1. *a*, a rhomboidal dodecahedron, and *b*, an elongated form of the same. *c*, a truncate dodecahedron, and *d*, a flattened form of the same (*a–d*, after Kieser). *e–i*, an orthic tetrakaidecahedron shown in its several aspects.

des végétaux, Paris, 1824, p. 49) succeeded in isolating the cells of pith by boiling them in nitric acid, and thus demonstrated that they are closed vesicles, independent though agglomerated. But of their shape he says merely,—"Their original form is globular; it is from the equality of the compression to which they are subjected in all directions that they often assume a symmetrical polyhedral form." It may readily be surmised why he did not describe the polyhedra in greater detail.

cells cut in serial sections, provided the cells are large enough and their walls distinct. Of human tissues, the epithelium lining the oral cavity is quite favorable, and reconstructions of eight cells have been completed; but the cells are small as compared with those of amphibians, and both small and irregular in contrast with cells of vegetable parenchyma. Hence the pith of the elder, *Sambucus canadensis,* was chosen. If a fresh moist specimen is obtained, it can be imbedded thoroughly in paraffin and cut in perfect series at a thickness of ten microns, thinner sections being undesirable. The chief difficulty will be in interpreting the cell walls which fall nearly in the plane of section and consequently appear as hazy films, but in ten-micron sections these will be dense enough to be recognized readily. Portions of pith were cut transversely and longitudinally, but the reconstructions were made exclusively from longitudinal sections. On the average a cell extended through sixteen of these sections. A small area of the tissue was drawn with the projection lantern at a magnification of 250 diameters, and selected cells in the drawing were enlarged by the pantograph to 500 diameters. After all the contacts had been studied and recorded, the models were made in wax by Ethel S. Lewis,— a task requiring patience and skill beyond that at the author's disposal. The most instructive of these models have been beautifully and accurately drawn by F. Schuyler Mathews.

The appearance of the cells in elder pith when sectioned lengthwise of the stem is shown in Figure 2. The long axis of the cells is transverse to that of the stem, contrary to the early statement of Hooke, but in accordance with a drawing by Dippel, who shows, however, that in the youngest internode in autumn the long axis may be perpendicular. Possibly after a period of rapid growth chiefly in length, the cells continue to divide transversely, thus becoming compressed and flattened, as found in the older internodes. The cells then have an accordion-like arrangement which is demonstrated by children in removing the pith by pushing it out of the stem. A long stretch may thus be cramped into a short space, but it regains almost fully its original length when released from the stem. It may well be that a similar but moderate contraction in the paraffin has rendered the cells modeled somewhat flatter than is normal, but this would not alter the number or shape of their contacts. The intercellular spaces, essential for the life of the cells, serve to blunt the edges and angles of the polyhedra, the form of which it is our purpose to make clear. Consequently these relatively small spaces (shown in Figure 2) have been disregarded. Further, the waviness of some walls, when evidently

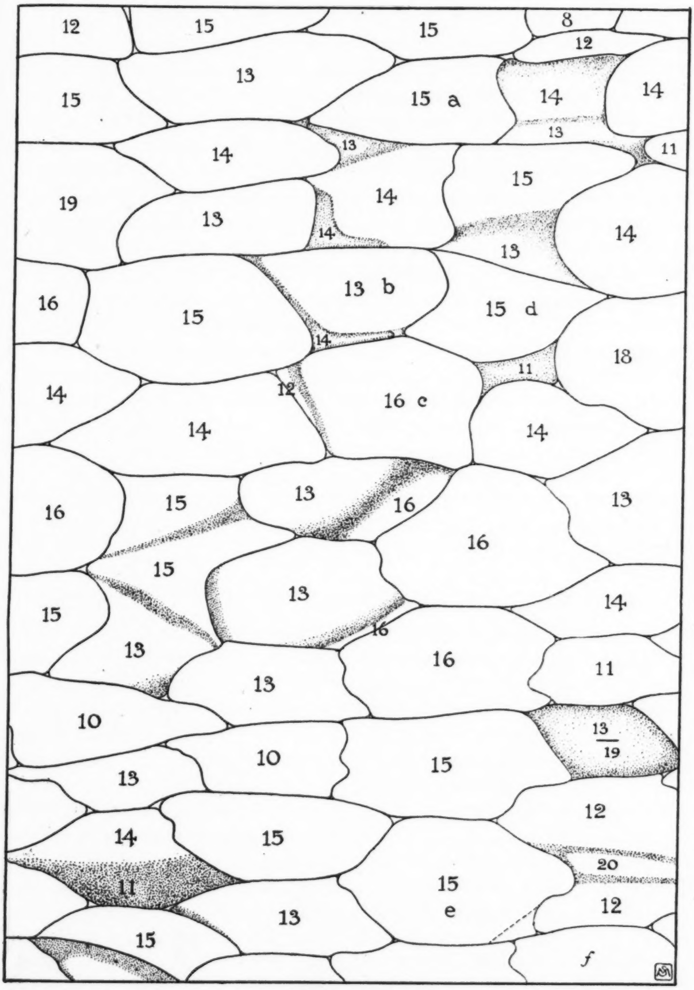


FIGURE 2. Longitudinal section of pith of the elder, *Sambucus canadensis*. × 220 diam. The numeral in each cell indicates the number of contacts which that cell has with other cells. Two numerals on a septum indicate the contacts of the cells above and below the septum. The letters are explained in the text.

due to shrinkage, has been deliberately smoothed out, altogether giving the models somewhat flatter surfaces and sharper edges than occurs in the preserved tissue. But this suppression of accidental irregularities has been permitted only when necessary to reveal the true pattern of the cell as indicated by its contacts with others.

The preliminary count of contacts which the cells have with those about them is partly recorded in Figure 2, by numerals placed within the cell outlines. Of the sixty-three cells there shown, the average number of contacts is 13.96. A contact is always a potential facet, and usually, as seen in the figure, is actually such. The contacts of thirty-seven more cells were counted, but, as it happened, the average number per cell remained unchanged — 13.96. In Table I is shown the number of cells, in the one-hundred counted, having the number of contacts indicated at the top of the several columns. The cells range from hexahedra to icosahedra, with no special tendency to form dodecahedra. More than half of them are 13-, 14- or 15-hedra. This is consistent with a typical tetrakaidecahedral form.

TABLE I.

No. of Surfaces	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
No. of Cells	1	1	2	0	2	8	8	21	16	19	10	2	3	6	1

Irregularities are due in part to the great difference in the volume of the cells. Calculated roughly from the displacement of the wax models, these cells ordinarily range in size from .0004 to .0014 c. mm., with an average volume very close to one one-thousandth of a cubic millimeter. Since such a cavity if filled with human blood would contain between four and five thousand corpuscles, it is evidently a cell of considerable size. The largest cell modeled measured .00224 c. mm., and the smallest was crowded and flattened to a mere .00008 c. mm. Cells with an excessive number of contacts are usually very large, and of such form as to suggest that an expected division in some particular plane has failed to occur. Thus they may be octagonal above and below, with two tiers of lateral surfaces, so that a vertical division would reduce them nearly to normal size and shape. Or they may be hexagonal above and below, with three tiers of lateral surfaces around most of their circumference; these would be reduced by a horizontal division. Certain instances of small cells with few contacts have resulted from an atypical division of cells approximately

tetrakaidecahedral, with subsequent arrest of development. The irregularities of the cells, due to their manner of growth, should not be underestimated. Among the forty-two cells modeled, there is not one with fourteen surfaces, eight of which are hexagons and six quadrilaterals, arranged as in the tetrakaidecahedron of Figure 1, and yet they seem to show convincingly that such is their typical shape, or the form from which they may all have been derived.

The typical shape is almost realized in a cell with fifteen contacts shown near the base of Figure 2 and labeled *e*. If its lower lateral wall on the right had taken the course of the dotted line in the figure, its fifteenth contact (with the cell *f*) would have been eliminated. This disturbing contact is shown as a small triangular area, *3*, in the basal view of the model, Figure 4 (Plate 1). It is there shown that the central hexagon is not surrounded by alternating quadrilaterals and hexagons, inasmuch as there are two adjacent pentagons on the left, and a third pentagon, due to the intrusion of the triangular surface *3*, on the right. The same cell, in lateral view, looking directly at the quadrilateral surface shown in Figure 4, is seen in Figure 5. Below the quadrilateral of the upper tier is a hexagon, and below the adjacent hexagon of the upper tier is a quadrilateral, which with the hexagon on the under surface are reproducing exactly the complex pattern of the type. Turning to a lateral view of this cell facing the adjacent pentagons of the upper tier, it is seen, in Figure 6, that there are also pentagons below them. If this cell were absolutely typical, its lower tier should present a succession of surfaces with the following numbers of sides — 4, 6, 4, 6 — whereas it does show 4, 5, 5, 6; and above them, in place of 6, 5, 5, there should be 6, 4, 6. But all these deviations would be rectified if the boundary between the pentagons in the upper tier were swung like a pendulum to the left, passing the boundary between the pentagons in the lower tier. In other words, differences in the relative volume of adjacent cells may convert two quadrilaterals and two hexagons into four pentagons. Thus it is seen that with the shifting of a single boundary and the elimination of a small triangular fifteenth contact, the cell shown in Figure 4 would be typical throughout.

It may be noted, however, that this cell is not at all an *orthic* tetrakaidecahedron, but, as if from flattening, the upper and lower tiers of lateral surfaces tend to meet at an equatorial ridge. In the orthic cells in the diagram, Figure 3, the squares make one third and the hexagons two thirds, of the distance from the top of the cell to the bottom; but in actual cells with an equatorial ridge, the squares almost

equal the hexagons in vertical measurement. A cell (Figure 2, *a*) with less of an equatorial ridge than that which has just been described, is shown in Figure 7. As seen by comparison with Figure 3, six of the seven surfaces which appear in the drawing are exactly according to the type.

A prolific cause of deviations from the tetrakaidecahedral form is found in the process of cell-division; and that this must be so, is evident upon reflecting that the division of a typical cell, whether vertical or transverse, reduces the number of surfaces from fourteen to eleven. Figure 11 is the pattern of vertical division through angles of the top and bottom hexagons, but the models afford no evidence that division in this plane actually takes place; Figure 12 shows vertical division through the sides of these hexagons; and Figure 9 illustrates transverse or horizontal division. With the completion of the process, a constriction occurs along the plane of division, whereby the daughter cells become more globular. In all cases the resulting cells have but eleven surfaces. Restoration of those which are lacking will depend upon the division of adjacent cells.

In elder-pith growth is chiefly in length, and division is predominantly transverse. The orientation of the cells, as will be seen, is in accordance with this. If the growth were chiefly in thickness, as in cork, it would be expected that the cells would be so turned that their inner and outer surfaces, instead of their upper and lower surfaces, would be hexagonal. In a typical cell oriented as in pith the transverse plane passes through hexagonal surfaces only, being above or below the quadrilateral surfaces in every case (Figure 9). If the cells in contact with the one which has thus divided, likewise divide transversely in the middle, the planes of their division will encounter the surfaces of the central cell as shown by the dotted lines in Figure 9. The position of these lines may perhaps be better understood by dividing several cells in the group shown in Figure 3 transversely through the middle. A line will pass across every lateral hexagonal surface, from square to square, bisecting the sides of the squares; and they cut off from each hexagon a small quadrilateral area, leaving the remaining portion still hexagonal. The contraction which follows the division of the adjacent cells produces ridges along the lines passing from square to square, and the tension or pull upon these squares converts them into hexagons. The diagram, Figure 8, shows, then, the restoration of the tetrakaidecahedral form, following the transverse division of the cell shown in Figure 9 and of those in contact with it, the corresponding surfaces in the two drawings being marked with the

same letters. Every square has become a hexagon, and is above or below a quadrilateral portion cut off from an original hexagon. Every hexagon of the original cell has produced a quadrilateral above and below, and its middle part remains hexagonal.

Can any such geometrical process be assumed to occur in actual cells? In Figure 2, at *b* and *c*, there are two cells which are shown inverted in Figure 10. Except that one of these has three more surfaces than the other (16 and 13 respectively) their configuration is suggestive of twins. On the side hidden in the figure each cell presents four surfaces meeting at a salient point, such tetrahedral angles being very exceptional and contrary to the arrangement of the experimental soap-films. There is also a striking duplication of surfaces shown in Figure 10, and they are so oriented as to indicate that this pair of cells resulted from a transverse division. The surfaces *a–e* would then correspond with those of the same letters in Figures 8 and 9. There is an additional fifth contact of *a* at *x:* typically this surface should be quadrilateral and its upper border horizontal. The surfaces *b* and *c* are in contact with one and the same cell and are typical, as are all four surfaces on the right. There a single cell is in contact with the quadrilateral and the hexagon below it. On the left, the upper hexagon is typical, but below it there are two surfaces instead of three, and these are in contact with a single cell. Evidently the cell corresponding with that adjoining *g, h,* and *i* in Figure 9 failed to divide with the rest. Consequently the surface *d* has five instead of six sides, and since the quadrilateral, *i*, is lacking, the entire cell has thirteen instead of fourteen contacts. The general arrangement of these faces is convincingly like the theoretical pattern.

Vertical division of the type shown in Figure 12 should produce a characteristic cell, having four pentagonal surfaces (two of which can be seen in the diagram, Figure 13) and a hexagonal face extending uninterruptedly from the top pentagon to the basal pentagon. Figure 14 represents an actual cell, which as seen from one side exhibits precisely these features. From other points of view it is not perfectly typical; yet it has exactly eleven surfaces, and clearly represents a cell which, after vertical division, failed to regain the tetrakaidecahedral form. Vertical division occurring directly over a cell dividing transversely would subdivide the hexagon beneath, producing on the top of the underlying cell an additional surface like that marked *x* in Figure 10.

Cells more difficult to interpret are shown in Figure 16, which represents a pair evidently derived from the transverse division of a

single predecessor. In one of their lateral aspects they present, as seen in the figure, four superimposed irregular pentagons, with angles jutting alternately to the left and right. The regularly superimposed quadrilaterals and hexagons on either side of them can not, by any change in the pentagons, be brought into harmonious relations with each other. It happens, however, that the cell shown in Figure 15 may explain the situation. This cell presents an atypical feature which is not very unusual, namely three, instead of two, superimposed lateral surfaces. A hexagon has a quadrilateral both above and below it. This would happen if the cell shown in Figure 9 failed to divide at the time when division took place in an adjoining cell at the plane indicated by the dotted line between *a* and *b*. This would convert the quadrilaterals *f* and *j* into pentagons; they would become hexagons through the transverse division of certain cells on the hidden side of the model. Thus the atypical features of the cell shown in Figure 15 may be satisfactorily accounted for. Now if this cell should divide transversely along the line of dashes, and adjacent cells against the faces *a* and *d* should divide along the dotted lines, a pair of cells almost identical with those in Figure 16 would result. The conditions in twelve of the thirteen surfaces there shown would be exactly reproduced. Division of a cell on the back of the model in Figure 15 would change the pentagonal surface *c* to a hexagon and make the analogy perfect.

There is sometimes evidence of an unequal cell division, as with the pair of cells shown in Figure 17. The cell from which they came was under the average size, and was pentagonal above and below, having twelve surfaces altogether. It exhibited a pronounced equatorial ridge. Transverse division took place below the ridge in a plane passing through a quadrilateral surface and separating scarcely more than one third of the cell from the rest. The volumes of the models are 55 c.c. and 30 c.c. respectively. In the drawing a dotted line indicates approximately the plane of normal division. As a result of the unequal partition, the upper cell retained a portion of all the original surfaces except that which formed the base, and with a new pentagonal basal surface, it continued to have twelve facets. The lower cell, however, has only eight facets, of which the three lateral ones shown in the figure extend continuously from the top to the bottom surfaces. The latter, as before mentioned, are pentagonal. On the side away from the observer, similar conditions obtain except that a small triangular fragment of one of the surfaces of the upper tier has been included in the lower cell.

The smallest cell observed, having a volume in the model of 10 c.c., was so very small and flattened that it required special examination to be sure it was not a distended intercellular space. That possibility could be definitely excluded. The model seems a formless body (Figure 19) yet one which may be tentatively explained as due to an unequal vertical division of a tetrakaidecahedron. The fragment of the pattern-model shown in Figure 18 has seven surfaces, but the actual cell in Figure 19 has but six. Four of these can be seen in the figure. The others are a very small triangular facet at the top of the hidden side, and a broad pentagonal area covering the remainder of that side. If the contact x in the pattern should be eliminated, there would remain six surfaces, each of which would have the number of sides actually found in the hexahedral cell.

Eleven of the forty-two cells modeled have now been considered, and it has been shown that great variations in the number, shape and arrangement of their facets are entirely consistent with a typical tetrakaidecahedral form. An equal division of a tetrakaidecahedron produces cells with only eleven surfaces; an unequal division may reduce the number still further, to eight or even seven, as has been shown by examples. On the other hand, if all the cells surrounding a particular tetrakaidecahedral cell should divide transversely, the undivided central cell would have three tiers of lateral surfaces and twenty contacts, the top and base remaining hexagonal. A cell among those modeled which closely approximates this form was evidently produced by a vertical division at a time when the cells around it divided transversely. If all the cells surrounding a particular cell, except the one immediately above it and the one immediately below it, should divide in halves vertically, and all in one plane passing through the sides and not the angles of the top and basal surfaces, then the central cell would be octagonal above and below; it would have sixteen lateral surfaces arranged in two tiers,— eighteen surfaces altogether; and there would be two points, on opposite sides of the cell, where four surfaces would meet, producing unstable tetrahedral angles. Such tetrahedral angles, made by the vertical bisection of a quadrilateral and of the hexagon above or below it as the case may be, would be the meeting place of two quadrilaterals side by side and two pentagons side by side, and precisely this grouping is seen in one of the models, in which the four surfaces meet at a salient point. Another model, being that of the largest cell studied, illustrates the entire configuration under discussion. Its upper surface is octagonal, and the two added borders are clearly the result of the bisection of two oppo-

site sides of the original hexagon, owing to the vertical division of the adjoining cells. The two tetrahedral angles produced by these vertical divisions have slipped into pairs of closely adjacent trihedrals. Among other irregularities this cell has an additional surface — nineteen instead of eighteen — but on the whole it is remarkably close to the theoretical pattern.

Another instance of this sort is seen in Figure 21 in connection with the large cell at the left of the group. Its two facets *a* and *b* result from the subdivision of a quadrilateral surface, caused by the vertical division of an adjoining cell. The constriction following this division drew out the angle between *a* and *b* on the top surface, and contributed one of the two extra sides possessed by the octagon. It may be noted that the plane of the ridge between *a* and *b* is continued downward by the plane of a vertical division which produced the surface *c*, but in such a way that the formation of a tetrahedral angle is avoided, as the surface *b* is pentagonal instead of quadrilateral. The large cell with the octagonal top in Figure 21, is in relation with similar large flat cells both above and below, thus forming a column which could be split, by vertical division, into two columns of cells of average size, with hexagonal instead of octagonal bases and tops. But the restoration of the tetrakaidecahedral form after vertical divisions is a complex process of readjustment, which cannot be explained by any simple scheme.

Thus far cells have been considered individually or in pairs. As a concluding observation, the mutual relations of cells in a group of seven (Figure 21) may be compared with those of a cluster of orthic tetrakaidecahedra shown in Figure 20. The pattern-group needs no explanation other than to note that the lowest cell in the midline has been cut in halves transversely. It could not, in wax, be made to constrict at its plane of division, so that it presents in the figure relatively a much larger upper surface than would occur in actual cells. The relative heights of the top surfaces of the cells in this pattern should be carefully observed. That of the central cell is at the lowest level. The distance from the central cell to the top of the half-cell in the midline below may be described as a half-step. Thence it is a half-step further up to the top of the cells on either side of it, which rise above the central cell by the width of a square. The distance from these to the tops of the cells seen above them in the figure, is a full-step, for these cells rise above the central cell by the width of a hexagon. They mark the highest plane in the drawing. Finally it is a step down from them to the top of the cell in the midline above.

The relative levels of the upper surfaces of all the actual cells shown in Figure 21 are like those in the pattern, Figure 20. Eighteen of the surfaces appearing in Figure 21 have been marked with figures indicating the number of their sides, and they correspond, both in respect to these numbers and in their relations to one another, with the eighteen surfaces similarly marked in the group of orthic tetrakaidecahedra.

The problem which it was undertaken to solve, by presenting actual examples for inspection, is that of the shape of cells when surrounded on all sides and compressed by similar cells. Elder-pith was selected as presumably typical of this condition, and so far as elder-pith is concerned, the cells are shown to be tetrakaidecahedra, modified, especially through cell-division, in rather definite ways. The surprisingly simple manner of restoring the tetrakaidecahedral form after the transverse division of an entire group of cells, was brought to light by the direct observation of the models. It is a pleasure to acknowledge the way in which the mathematicians and physicists have anticipated our principal conclusion; yet in such shapes as we have found, they may not recognize the verification of their calculations and experiments.

Literature Cited.

Berthold, G. Studien über Protoplasmamechanik. Leipzig, 1886. p. 1–332. Especially chapters 7 and 8.

Buffon, M. de. Histoire naturelle. Nouvelle édition. T. 5. Paris, 1769. p. 379–380.

DeCandolle, Aug. Pyr. Organographie végétale. T. 1. Paris, 1827. p. 13.

Dippel, L. Beiträge zur Histologie der Pflanzen. Verh. d. naturhist. Ver. d preuss. Rheinlande u. Westphalens. Jahrg. 22, 1865. Botanik, p. 1–9.

Errera, Léo. Sur une condition fondamentale d'équilibre des cellules vivantes. Comptes rendus de l'acad. des sciences, T. 103, Paris, 1886. p. 822–824. Also in the Bull. de la Soc. Belge de Microscopie, T. 13, 1887. p. 12–16.

—— Ueber Zellenformen und Seifenblasen. Tageblatt d. 60 Vers. deutscher Naturforscher u. Aerzte in Wiesbaden, 1887, p. 246–249.

Grew, Nehemiah. The Anatomy of Plants. 2d ed. London, 1682. p. 64, 76 and 120.

Hooke, R. Micrographia. London, 1665. p. 115–116.

Kelvin, William Thomson, *1st baron.* On the division of space with minimal partitional area. Philosophical Mag., vol. 24, 5th series. London, 1887. p. 503–514.

—— Baltimore lectures on molecular dynamics. London, 1904. p. 615.
—— The molecular tactics of a crystal. Robert Boyle Lecture. Oxford, 1894. p. 21–25.

KIESER, DIETERICH GEORG. Mémoire sur l'organisation des plantes. Harlem, 1814. p. 89.
—— Grundzüge der Anatomie der Pflanzen. Elemente der Phytonomie. Erster Theil. Phytotomie. Jena, 1815. p. 9–10, 40–44, and Taf. I.

OKEN, LORENZ. Elements of Physiophilosophy. Ray Society, London, 1847. p. 209.

PLATEAU, J. Statique expérimentale et théorique des liquides. T. 1. Paris, 1873. Especially Chapter 5.

THOMPSON, D'ARCY WENTWORTH. On growth and form. Cambridge, 1917. Chapter 7, especially p. 336–339.

EXPLANATION OF PLATES.

PLATE I.

FIGURE 3. A group of orthic tetrakaidecahedra.
FIGURES 4, 5, and 6. Three views of a model of cell *e* in Figure 2, having fifteen surfaces. × 275 diam.
FIGURE 7. Model of cell *a* in Figure 2, having fifteen surfaces. × 333 diam.

PLATE II.

FIGURES 8 and 9. Orthic tetrakaidecahedra utilized to show the restoration of the original form following transverse division.
FIGURE 10. Model of a pair of cells, evidently resulting from a transverse division, lettered to correspond with Figures 8 and 9. The upper cell has 16 contacts, the lower, 13, being cells *b* and *c* of Figure 2, inverted. × 266 diam.
FIGURES 11 and 12. Orthic tetrakaidecahedra divided vertically through the angles, and through the sides, respectively, of their top and basal surfaces.
FIGURE 13. The right half of Figure 12, for comparison with Figure 14.
FIGURE 14. Model of a cell with 11 surfaces, produced from a tetrakaidecahedron by vertical division. × 333 diam.
FIGURE 15. Model of a cell with 18 surfaces, which through transverse division, accompanied by that of certain adjoining cells, would produce conditions similar to those in Figure 16. × 250 diam.
FIGURE 16. Model of a pair of cells, evidently resulting from a transverse division, showing atypical features explained in the text. × 225 diam.
FIGURE 17. Model of a pair of cells resulting from an unequal transverse division. × 333 diam.
FIGURE 18. Portion of an orthic tetrakaidecahedron for comparison with Figure 19.
FIGURE 19. Model of a small flattened cell having six surfaces. × 270 diam.

PLATE III.

FIGURE 20. A group of orthic tetrakaidecahedra for comparison with Figure 21.
FIGURE 21. A group of seven cells (the central cell being *d* of Figure 2) showing 18 surfaces which correspond in position and the number of their sides with those bearing numerals in Figure 20. × 260 diam.

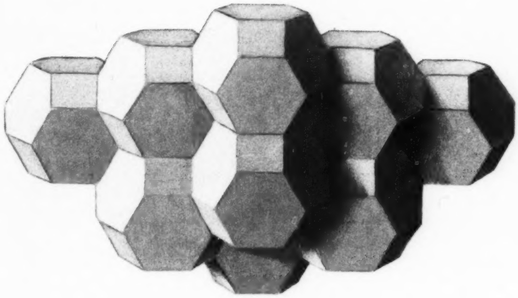


Fig. 3

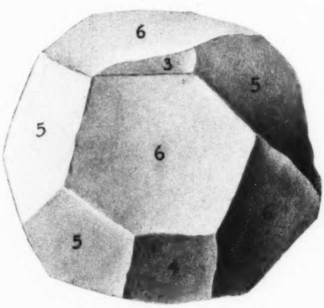
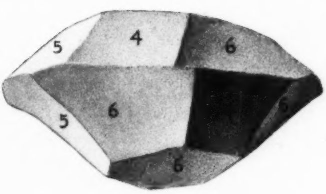


Fig. 4



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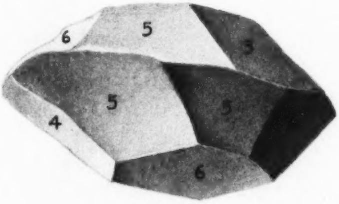

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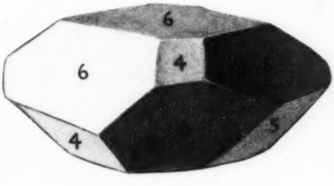

Fig. 7

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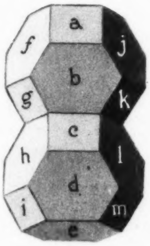

Fig. 8

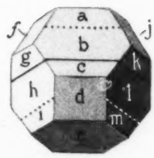

Fig. 9

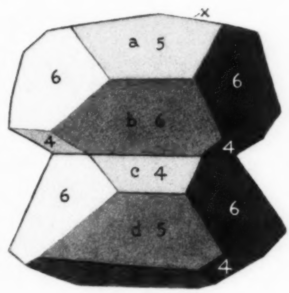

Fig 10

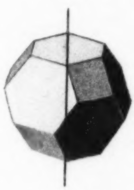

Fig. 11

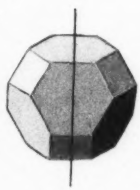

Fig. 12

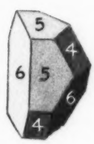

Fig. 13

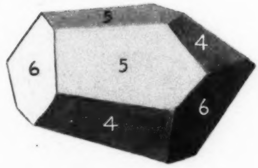

Fig. 14

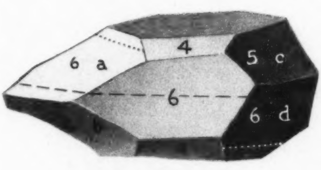

Fig. 15

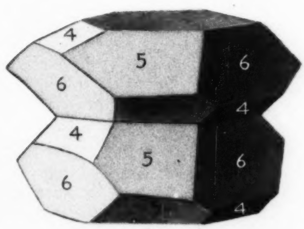

Fig. 16

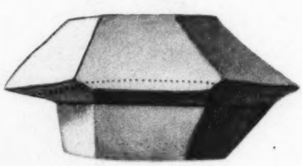

Fig. 17

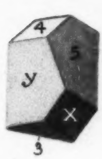

Fig. 18

Fig. 19

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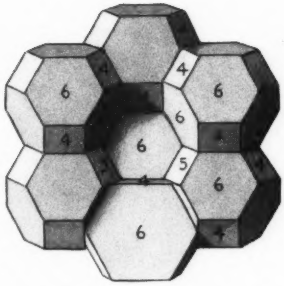

Fig. 20

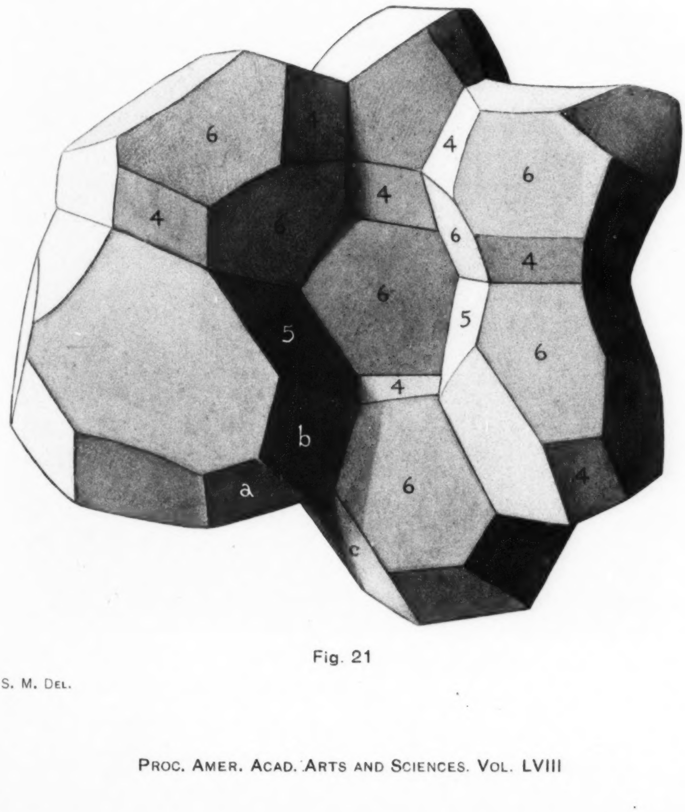

Fig. 21

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